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PALEONTOLOGY.—*The crossopterygian hyomandibular and the tetrapod stapes.*[1] THEODORE H. EATON, JR., Union College, Schenectady, New York. (Communicated by C. LEWIS GAZIN.)

Romer's description, in 1937, of the braincase of *Megalichthys*, a Permo-Carboniferous crossopterygian fish, showed that the hyomandibular bone articulated with the otic region by two heads, one dorsal and one ventral to the jugular vein. This arrangement, elsewhere unknown in vertebrates, had been anticipated in part by Schmalhausen, DeBeer and Watson. They could not, however, attribute the two-headed hyomandibular to any particular fish, and their hypotheses differed greatly in details. The views of Schmalhausen and DeBeer were summarized by Goodrich (1930) in his *Studies on the structure and development of vertebrates,* and those of DeBeer again by Romer (1937). Watson's related suggestion is in his paper on the origin of Amphibia (1926).

In the summer of 1937 I had the privilege of studying the *Megalichthys* material with Dr. Romer and attempting to restore some of

the soft anatomy. This paper presents two suggestions: (1) That the articulations of the hyomandibular are carried over essentially unchanged, and may be identified, in the connections of the stapes with other skeletal parts in most tetrapods, and (2) that the stapedial muscle is not limited to mammals but probably came up in their ancestry from the anterior edge of the levator hyoidei of fishes. Most of the data are from published sources, but I have added to them a series of simple reconstructions and two or three new observations.

Figure 1 is a diagrammatic reconstruction of the hyomandibular of *Megalichthys* and its relations to other parts. The attachments to skeletal parts are numbered arbitrarily: 1 the dorsal process, to the parotic region of the cranium above the jugular canal, 2 the ventral or otic process, below the jugular canal, 3 the connection with the ceratohyal, 4 that with the quadrate, and 5 with the operculum. The latter two connections are not represented by distinct processes, but were undoubtedly present as close attachments in all generalized hyostylic operculate fishes. Above the groove for the jugular vein, on the posterior part of the otic region, is a smooth muscle scar, which could only be for the levator hyoidei, likewise present in generalized hyostylic fishes. Whether this muscle extended as far down as the mandible is not determined, so that its restoration is conservative. In Amphibia, however, the levator hyoidei is largely converted into the depressor mandibulae by shifting its insertion to the posterior end of the lower jaw.

Three brief comparisons with the arrangement in other fishes will show that this type of hyomandibular occupies, probably, a fairly central, primitive position in the evolutionary scheme. Figure 2 indicates the corresponding structures in a dissection of *Squalus*, a shark. The articulation with the cranium is single and ventral to the jugular vein. Probably it is equivalent to no. 2, and no. 1 is either primitively or secondarily absent. No. 5 probably never existed, as there is no evidence that sharks ever had a bony operculum.

In the advanced fishes, Actinopteri, the hyomandibular articulates with the braincase above the jugular vein instead of below, and presumably articulation 2 has been lost, on the assumption that the double-headed hyomandibular is ancestral for these fishes. Numbers 3, 4 and 5 are, of course, regularly present.

The Dipnoi, lungfishes, make a more difficult problem, as the hyomandibular is so far reduced as to be almost unrecognizable in the adult, and has lost practically all its primitive connections. But even here, in the embryo of *Neoceratodus* (Fig. 3), we may possibly see a

remnant of a double cranial attachment with the jugular vein between, and also one to the quadrate and another for the ceratohyal. If this be the correct interpretation, the only one of our five connections actually missing is that for the operculum. In modern Dipnoi, at least, the operculum is greatly reduced and depends primarily upon its extensive muscle sheet for support.

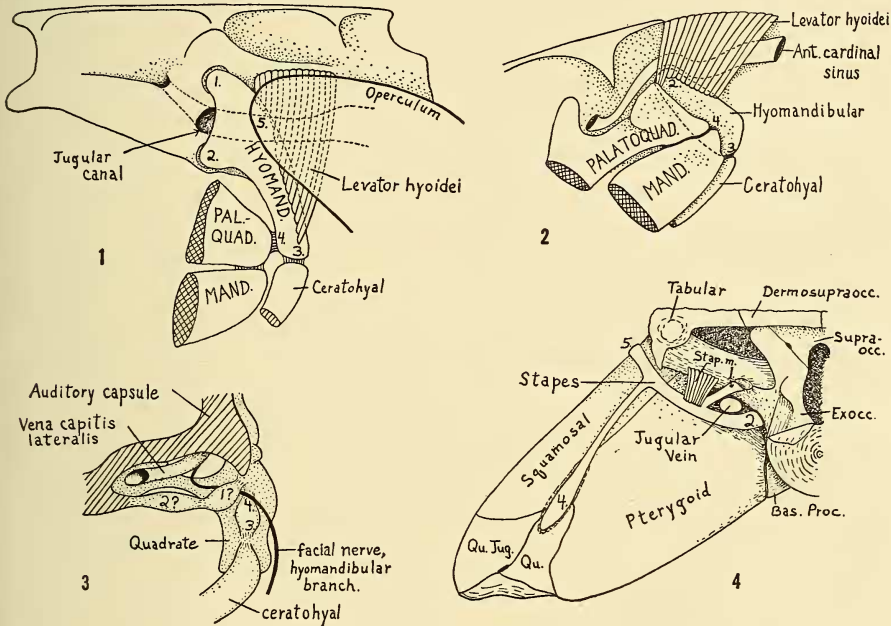Enough has been said to show that Romer's discovery may be the

Fig. 1.—Crossopterygii: *Megalichthys*. (Adapted after Romer, 1937.) Left lateral view.   Fig. 2.—Elasmobranchii: *Squalus*. Left lateral view.   Fig. 3.—Dipnoi: *Neoceratodus*, embryo, 18.5 mm. (Modified after Goodrich, 1930.) Posterior view, right side.   Fig. 4.—Embolomeri: *Orthosaurus*. (Based on Watson, 1926.) Posterior view, left side.

means of settling the long dispute over homologies of the hyomandibular and its cranial articulations in fishes. Turning back to *Megalichthys* again, the prevailing opinion for some years has been that Crossopterygii stand very close to the ancestry of tetrapods, and it should be profitable to make as detailed a comparison as possible between the hyomandibular and the amphibian stapes.

Figure 4 is a composite reconstruction of the stapes in the embolomerous Stegocephalia, based partly on Watson's figures and partly on his descriptions (1926). On the lower portion of the otic capsule the foot of the stapes rested in a pit, which, however, did not pene-

trate the capsule wall. He calls it the pseudofenestra ovalis. It is clearly an early stage in the evolution of a complete fenestra into the otic cavity, but presumably sound could already be transmitted by way of the stapes. Watson says he believes a dorsal process to have been present in Embolomeri, and also one to the quadrate, both of them doubtless cartilaginous. There is a small pit on the quadrate, sometimes at the point where the squamosal, pterygoid and quadrate meet (*Orthosaurus*), facing towards the otic capsule, and showing the location of the process from stapes to quadrate. Above the pseudo-fenestra ovalis there is a concavity along the side of the braincase which is the probable location of the jugular vein. In modern Amphibia and Reptiles this vein is above the fenestra ovalis and the foot of the stapes. It would seem, then, that the foot of the stapes, transmitting sound to the ear cavity, can be nothing but the ventral cranial articulation, no. 2, of the fish hyomandibular; that the dorsal process to the parotic region of the cranium is no. 1; that the quadrate connection, no. 4, is present as a cartilage rod in some cases. No doubt during ontogeny the hyoid attachment, no. 3, is temporarily present; whether it continued through life in a ligamentous form is, of course, impossible to say. But we still have one end unaccounted for. In Stegocephalia this end extended outwards in the otic notch to the level of the skin, that is, to the ear drum. Connection no. 5, to the operculum in Crossopterygii, was located on the outer face of the hyomandibular, therefore certainly nearest to the skin, as the operculum was a superficial, dermal bone. When the operculum disappeared, with the transition to land life, this part of the hyomandibular might most readily have been left attached to the integument and have served to receive sound vibrations from outside, while that area of the integument became the ear drum. Watson remarks that the bony stapes of Embolomeri seems to lie at right angles to that of, for instance, *Osteolepis*, the Crossopterygian which he used for comparison. We can see that this is not so much a shifting of position of the bone as the development of a new axis, namely from the fenestra ovalis to the otic notch instead of from the parotic process to the ceratohyal.

The bulk of the levator hyoidei muscle of Crossopterygii had, with the reduction of the hyomandibular, changed its insertion to the mandible, being known from now on as the depressor mandibulae. But there can be little question, on the basis of evidence from certain reptiles and from mammals, that in early Stegocephalia a slip of this muscle continued to insert on the stapes, its origin being somewhere close to the parotic process and its course being external to the jugu-
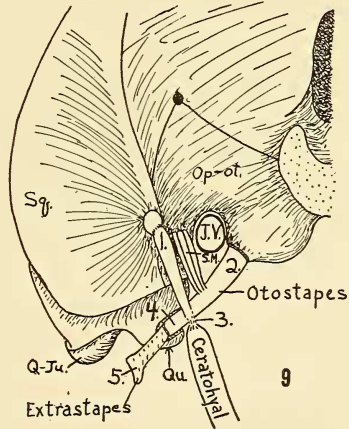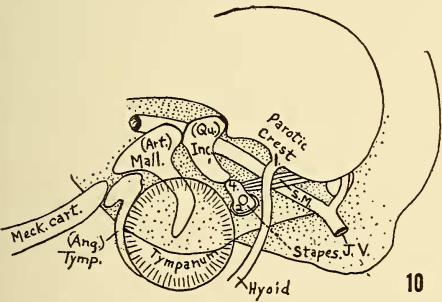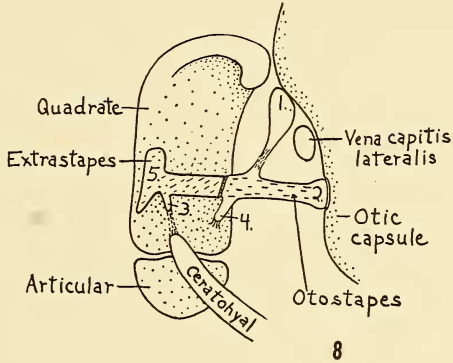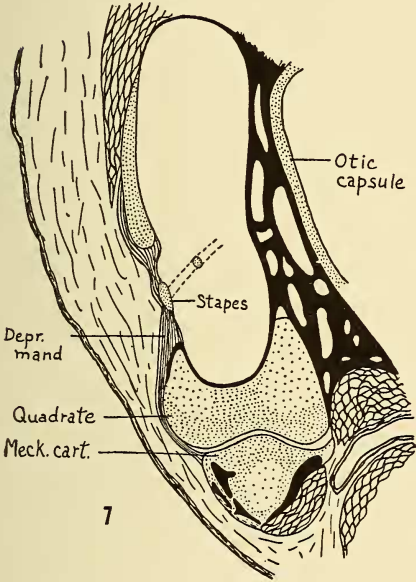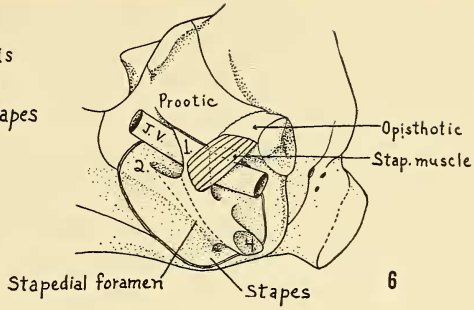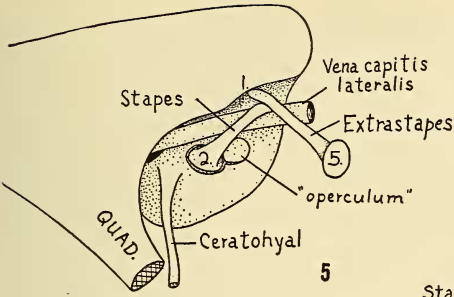
Fig. 5.—Anura: *Rana catesbeiana*. Left lateral view.   Fig 6.—Cotylosauria: *Captorhinus*. (Adapted after Price, 1935.) Left lateral view.   Fig. 7.—Chelonia: *Chrysemys marginata*. (Just hatched, C. L. 25 mm.) Left otic capsule, transverse section.   Fig. 8.—Lacertilia. Generalized diagram. Posterior view, left side.   Fig. 9.—Theriodonta: *Kannemeyeria*. (Adapted from Pearson, 1924.) Posterior view left side.   Fig. 10.—Marsupial embryo. Generalized diagram. Left lateral view.

lar vein. This is the ancestral stapedial muscle, which does not seem to be limited strictly to mammals, and which receives a branch of the facial nerve, as it should according to this scheme.

Among modern Amphibia the stapes of the adult contributes little to knowledge of the auditory region of any other types. In Caecilia and Urodela it is much reduced and even the ear drum itself is secondarily lost, while in some Urodela a substitute apparatus develops to transmit sound to the ear by way of the shoulder girdle. In Anura, however, something more like the primitive condition exists (Fig. 5). The bony stapes fits into the fenestra ovalis beneath the jugular vein. Laterally, reaching to the ear drum, is a cartilaginous extrastapes, which may be considered a modification of the distal end of the stapes itself. This, near the point where the bony part begins, connects with the parotic crest dorsal to the tympanic cavity and jugular vein (no. 1). Temporarily, during development, strands of procartilage reach to the quadrate and the ceratohyal, but the latter presently fuses to the cranium, as shown. There is no stapedial muscle in the modern Amphibia, and their auditory structure is definitely off the line which led to higher forms. But we can see that the five points of attachment already described persist in the Anura, three of them in the adult.

One of the oldest reptiles on which any information about the stapes has been obtained is the Cotylosaur *Captorhinus* (Fig. 6). The braincase was described and carefully figured by Price (1935). The stapes, a relatively large one, was perforated by a canal for the stapedial artery. The expanded foot (no. 2) fitted the fenestra ovalis beneath the jugular canal, and a slender dorsal process (no. 1) articulated with the prootic. Judging from other Cotylosaur material (e.g., *Labidosaurus*, Williston, 1910), the distal end of the stapes reached the corner of the quadrate at the junction of the latter with the pterygoid, or connected with it by a cartilage process. Evidently there was a cartilaginous extrastapes, for otherwise the stapes, as shown, could not have served for sound transmission. On the anterior face of the dorsal process (no. 1) Price found in *Captorhinus* "indications of a strong ligamentous or muscular attachment." Whether ligamentous or muscular, this structure was probably the stapedial muscle or its vestige, and I have shown its possible position in this figure.

An interesting bit of evidence on the stapedial muscle occurs in embryo turtles, for example in *Chelydra* and in *Chrysemys* (Fig. 7). A section made through the tympanic region of the latter at the time of hatching shows the anterior edge of the depressor mandibulae mus-

cle attached directly to the end of the extrastapes, but at the same time continuing down to the lower jaw. This connection, which I would interpret as a passing remnant of the attachment of a separate muscle to the stapes, disappears shortly, but is represented in adult turtles by a short ligamentous connection of the depressor muscle to the cartilage rim of the ear drum cavity.

The condition in some lizards closely resembles our reconstructed Stegocephalian and Cotylosaur ear, and all five of the primitive attachments of the stapes occur during ontogeny (Fig. 8). No. 1, the dorsal process, develops in temporary connection with the body of the stapes, lies externally to the jugular vein, and finally separates as an "intercalary" cartilage. An opposite process (no. 4) goes to the quadrate and usually persists through life. Temporarily the stapes is connected with the ceratohyal (no. 3). No. 2 and no. 5 are present as the functional inner and outer ends of the stapes, just as in Embolomeri, but no. 5 is cartilaginous (an extrastapes).

Before considering the somewhat more difficult problem of the mammalian ear it is necessary to try restoring the complete stapes of a Theriodont, if possible, from the work of Broom, Watson and others. Since very few of the known mammal-like reptiles have much of the auditory apparatus remaining in the fossils, we must select one which happens to show it most clearly, without regard for the particular line which may lead to mammals.

A diagram of an occipital view of the ear region in the Anomodont *Kannemeyeria* (based on Pearson, 1924) will suggest two or three important changes which took place as the mammalian ear evolved (Fig. 9). The stapes was a short, bony rod reaching from the fenestra ovalis to the inner edge of the quadrate, where its distal end rested in a groove. There was undoubtedly, as in other reptiles, a cartilaginous extrastapes, although it need not have been long, for the ear drum may have been slightly sunken into a canal already. The quadrate itself was in the process of reduction and formed only the inner portion of the jaw articulating surface. The fenestra ovalis, and therefore the foot of the stapes, was ventral to a deep notch in which it is safe to say the jugular vein passed. The whole auditory apparatus had come farther ventrad and mediad than in amphibians or other reptiles. There is a distinct parotic process on the border between the squamosal and opisthotic. Lateral to this, on the squamosal, was a broad trough providing an origin for the depressor mandibulae. Considering that the parotic process in earlier types receives articulation no. 1 (the dorsal process) from the stapes, and that it is external to

the jugular notch, I think that we may look for a homologous struc-
ture to attach to the same place in some of the mammal-like reptiles,
that is, a dorsal process from the stapes or its equivalent. We may
also suspect that the stapedial muscle originated on the face of the
opisthotic just inward from the parotic process.

If the interpretation is correct so far it should not be too great a
jump to the stapes of a primitive mammal in an embryonic stage (Fig.
10). The dorsal end of the hyoid arch becomes attached very early
to the parotic crest dorso-laterally from the stapes proper, and ex-
ternally to the jugular vein. This end of the hyoid is then called
laterohyal or stylohyal. Goodrich (1930) noted its similarity to the
dorsal process of reptiles. I suggest that this dorsal process of the rep-
tilian stapes has detached itself, during the early evolution of mam-
mals, from the remaining portion of the stapes, and associated with
the hyoid alone (connection no. 3). It is possible, then, that in *Kan-
nemeyeria* and its relatives the dorsal process was already becoming
a so-called "stylohyal" and supported the ceratohyal directly, while
the inner part of the stapes, with its extrastapedial, was more com-
pletely freed for auditory transmission. The stapes of mammals has
lost the extrastapedial because the quadrate and articular moved into
the ear cavity and took its place. The stapedial muscle, becoming al-
most microscopically small, is still associated in mammals with the
auditory stapes proper.

The associations of parts, then, in the mammalian ear, are new, but
the old morphological features of reptiles, amphibians and even fishes
are still there and may be recognized, according to this theory. It may
be that with the evolution of a mammalian larynx, and mobile mus-
cular tongue, along with chewing movements of the lower jaw, there
was reason for a more sturdy attachment of the hyoid arch to the
cranium, and the most convenient method of obtaining it was by
annexing the dorsal process of the stapes. At the same time the re-
mainder of the stapes came to depend on the quadrate, while the lat-
ter was still in the upper jaw, for a more complete support than it
had in amphibians or most reptiles, and thus drew closer the original
attachment no. 4. At some time, as Broom pointed out (1912), there
must have been a double articulation between the mandible and the
upper jaw, consisting not only of the old joint between the quadrate
and articular but of a new one between squamosal and dentary. In
time the latter survived, while the quadrate and articular, being very
close against the ear drum, were drawn into the auditory complex and
replaced the old cartilaginous extrastapes.

Summary.—The crossopterygian hyomandibular bone, evolving into the tetrapod stapes, retains its original morphological relations largely unchanged, even to mammals. New functions and new locations of parts appear, but the connections, I suggest, remain essentially as follows: 1. The dorsal cranial head of the hyomandibular becomes the dorsal process of the stapes, and, in mammals, the so-called stylohyal. 2. The ventral head of the hyomandibular, below the jugular vein, becomes the foot of the stapes and occupies the fenestra ovalis. 3. The connection of the hyomandibular with the ceratohyal generally does not persist beyond early developmental stages in tetrapods, but apparently in the line leading to mammals the ceratohyal was still able to link itself to the cranium through the dorsal process of the stapes. 4. In many types the attachment to the quadrate disappears except in early development, but it was shown to be present in early Stegocephalians, Cotylosaurs, lizards and the mammal-like reptiles, while in mammals it becomes the joint between the stapes and the incus. 5. The attachment of the hyomandibular to the operculum in fishes seems to furnish a convenient point for that between the stapes and ear drum in early tetrapods. Later this end of the stapes became cartilaginous and was finally atrophied in the transition from reptiles to mammals.

The levator hyoidei muscle became split, in Amphibia, into a large depressor mandibulae and a small stapedial muscle, the latter probably being limited to certain Stegocephalia. Traces of the stapedial appear in some primitive reptiles, and in mammals it is regularly present, while the depressor mandibulae serves the Amphibia, reptiles and birds, but in mammals is replaced by the digastric.

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